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Optimality in Neural Adaptation

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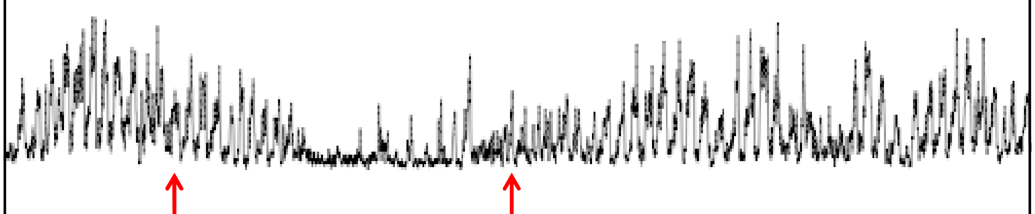
Encoding signals in context



Signals occur in a time-varying statistical context

Multiple codes:

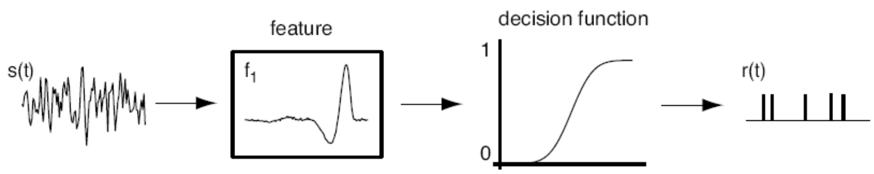
• Different components of the stimulus are encoded at different timescales with different coding strategies

• Fluctuations and context (phase and envelope) are encoded separately

Optimal neural coding

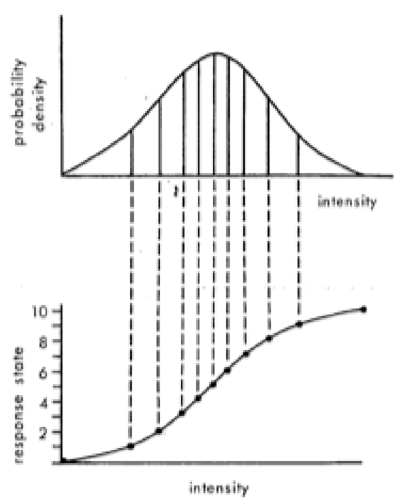
- Information maximization in dynamic response properties
- From system to single neuron
- The biophysics of efficient coding

Neural encoding model



Optimal coding hypothesis

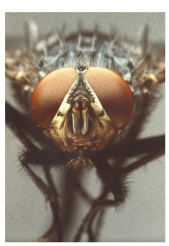
- Sensory systems attempt to maximize information transmission
- Should maximize efficient use of available response bandwidth



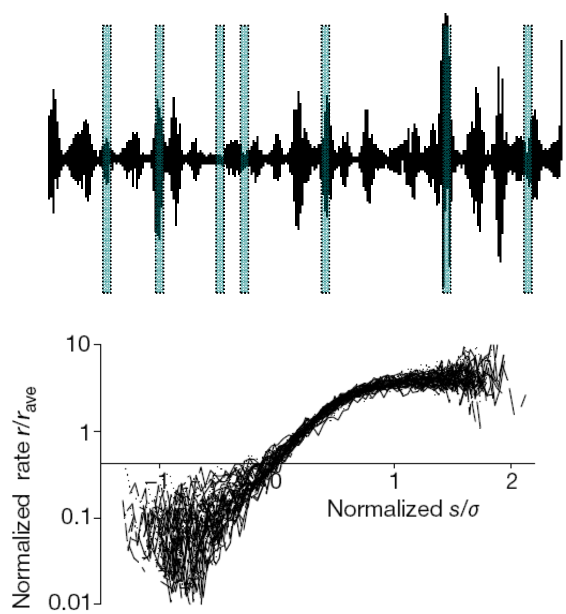
Laughlin, 1981

Dynamically optimal coding

Normalized stimulus representation in the fly visual system

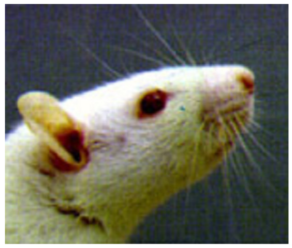


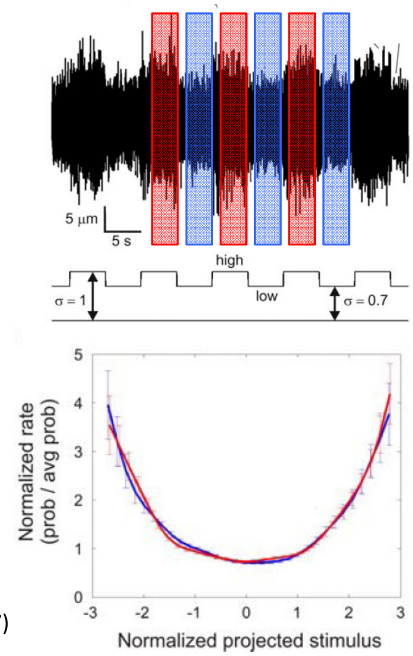
For fly neuron H1, determine the input/output relations throughout the stimulus presentation



A. Fairhall, G. Lewen, R. R. de Ruyter and W. Bialek (2001)

Normalized stimulus representation in rat barrel cortex

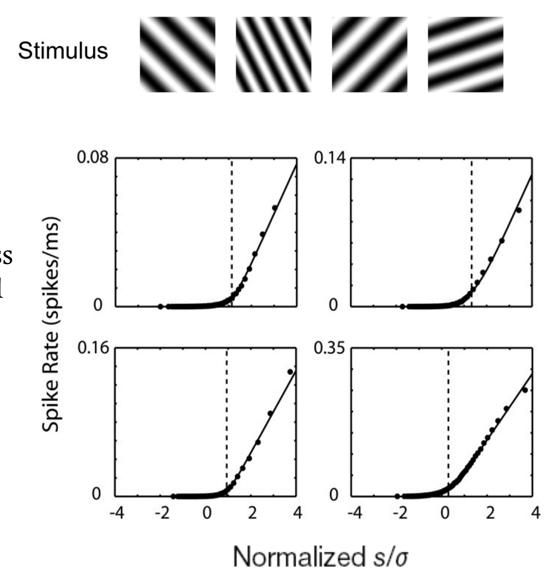




Extracellular *in vivo* recordings of responses to whisker motion in rat S1 barrel cortex in the anesthetized rat

M. Maravall et al., PLoS Biology (2007)

Normalized stimulus representation in monkey V1

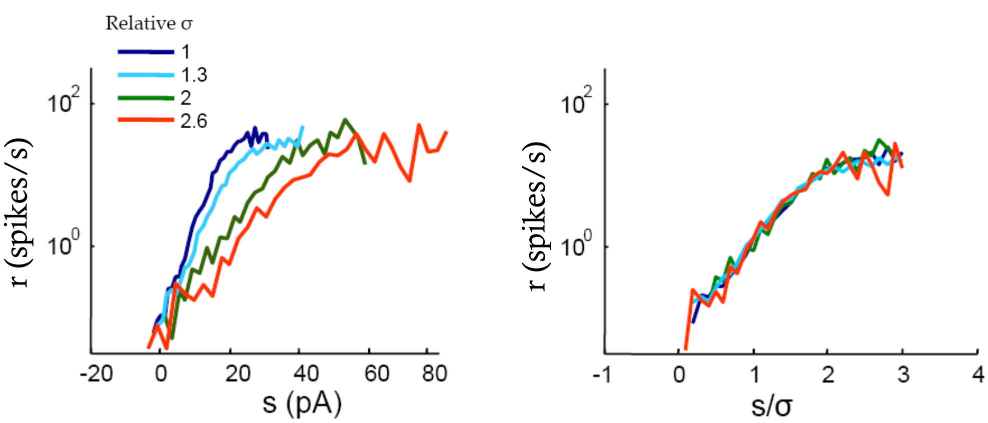


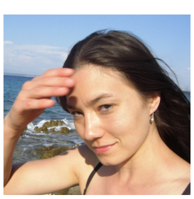
Consistent response functions across stimulus distributions and neuronal population

Ringach and Malone (2007)

What produces this normalized representation?

Normalized input representation in single cortical neurons





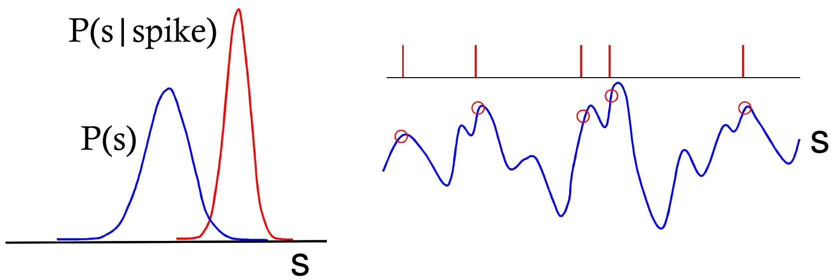
R. Mease, A. Fairhall and W. Moody, submitted

Quantifying scaling

The input/output function is, from Bayes' rule:

P(spike | stimulus) = P(stimulus | spike) P(spike) / P(stimulus)

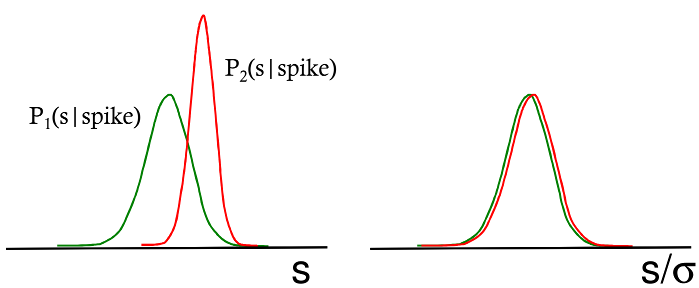
Replace stimulus **s**(t) with scalar value s_1



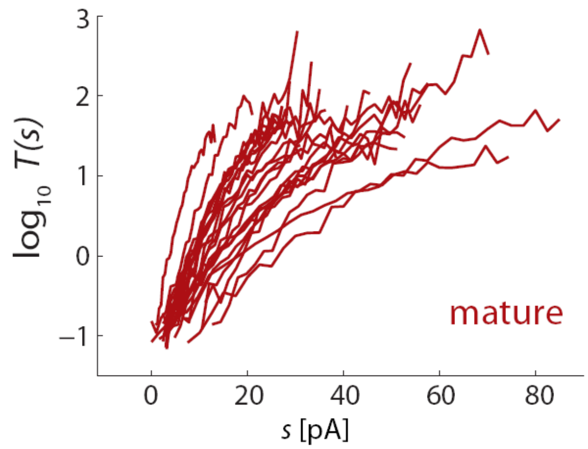
Quantifying scaling

P(spike | s) = P(s | spike) P(spike) / P(s)

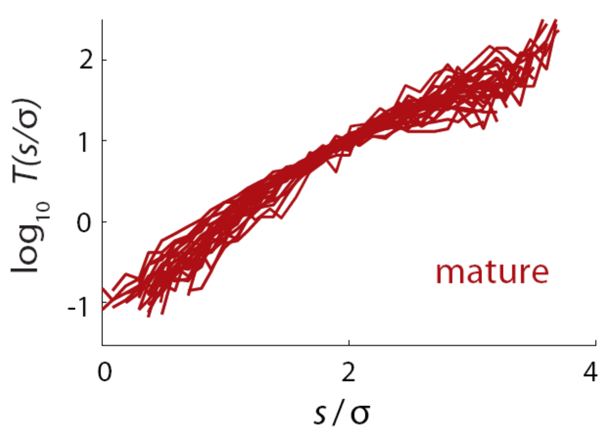
Distance measure: $D_{KL}(P_1(s/\sigma \mid spike) \mid P_2(s/\sigma \mid spike))$



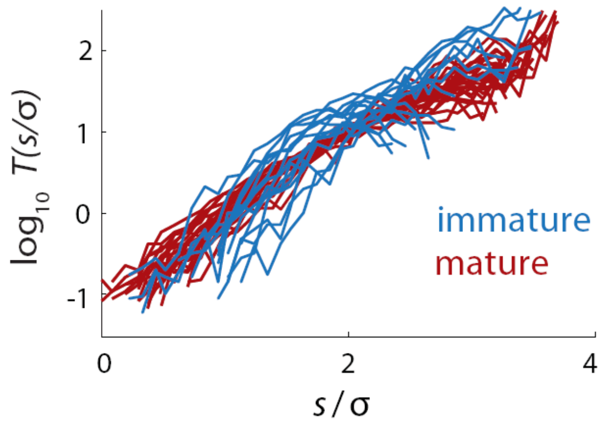
This normalized representation emerges in development



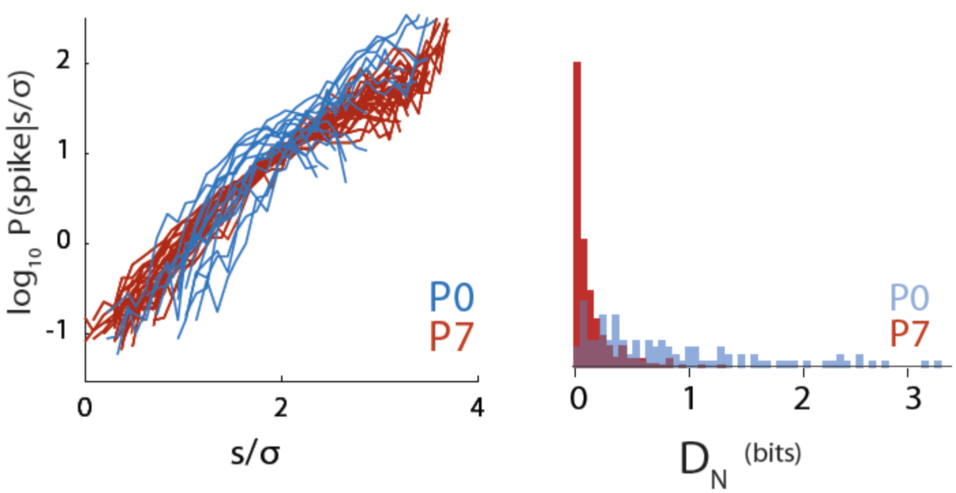
At P7, the population exhibits a common threshold function



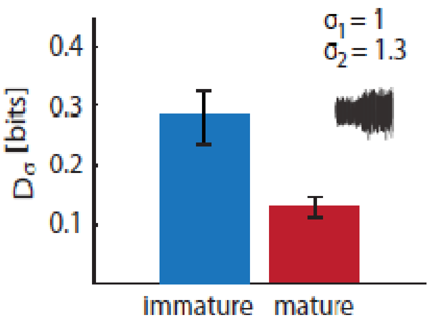
At P0, threshold functions are variable

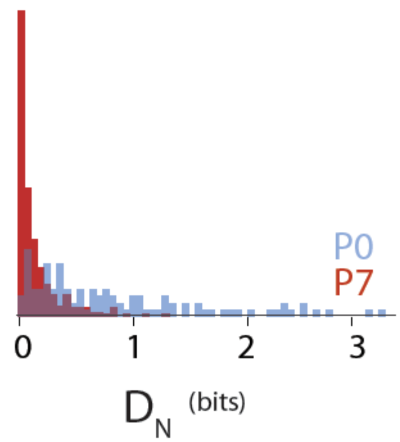


This normalized representation emerges in development

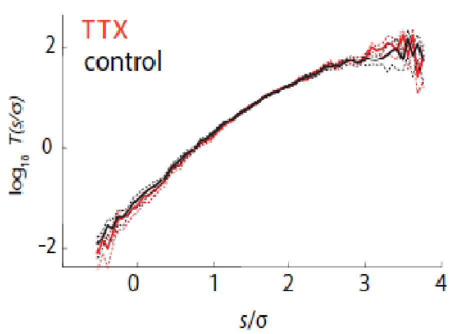


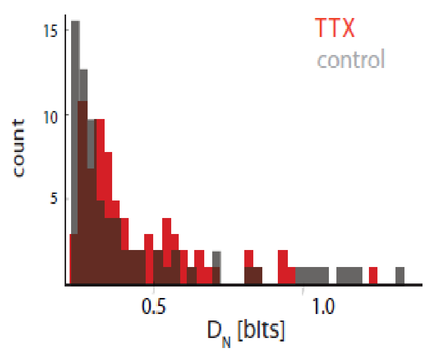
This normalized representation emerges in development



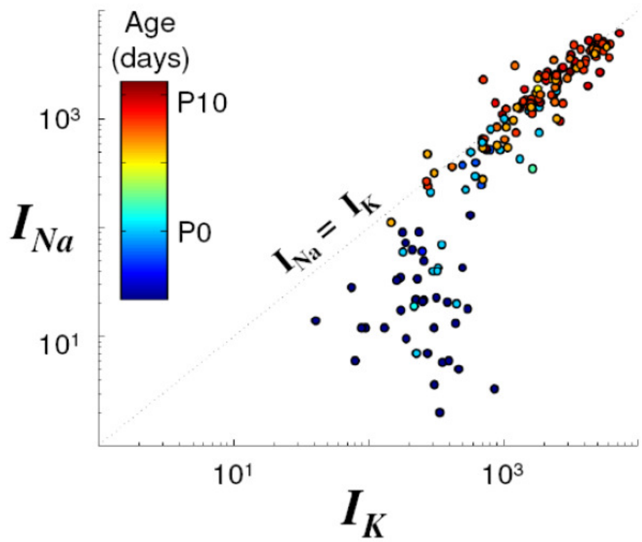


Is it activity-dependent?

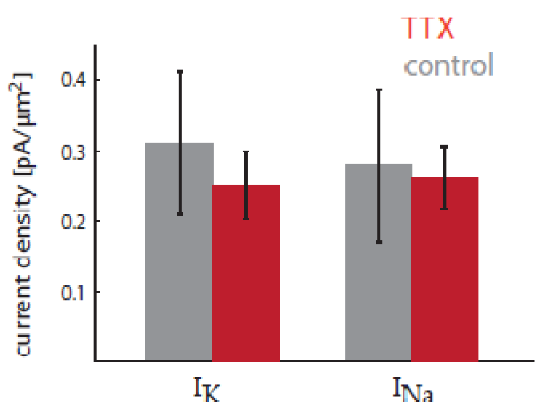




What needs to be true for this to happen?



Activity-dependent?



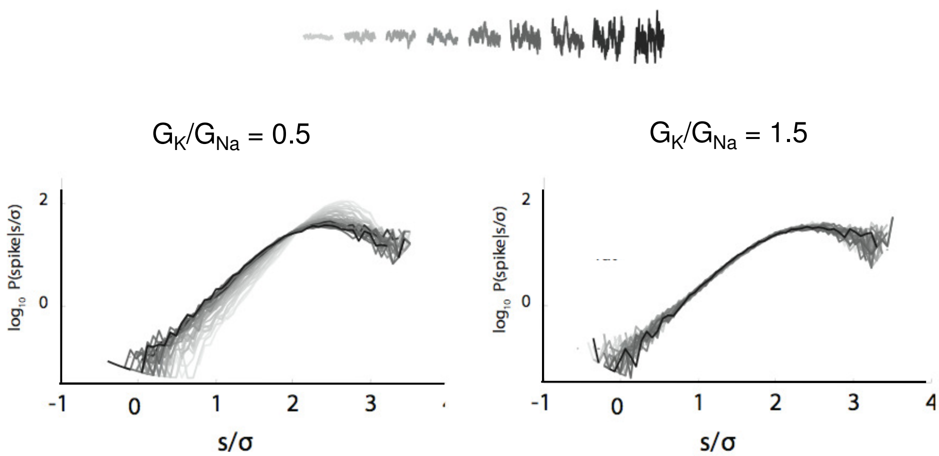
Coincidence or cause?

Somatic model parameters leading to gain scaling

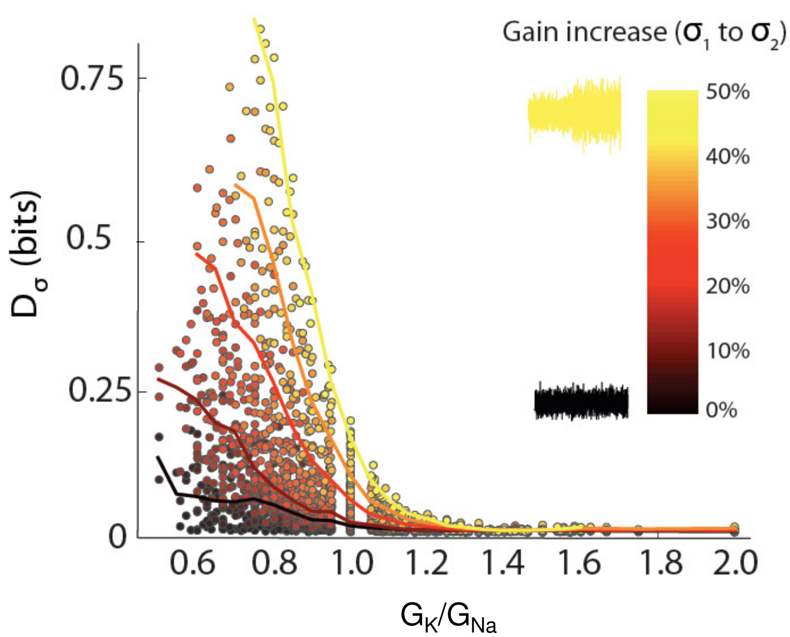
$$C\frac{dV}{dt} = I(t) - \bar{g}_{\mathrm{K}} n^4 \left(V - V_{\mathrm{K}}\right) - \bar{g}_{\mathrm{Na}} m^3 h \left(V - V_{\mathrm{Na}}\right) - \bar{g}_l \left(V - V_l\right)$$

$$\begin{aligned} dn/dt &= \alpha_n(V)(1-n) - \beta_n(V)n \\ dm/dt &= \alpha_m(V)(1-m) - \beta_m(V)m \\ dh/dt &= \alpha_h(V)(1-h) - \beta_h(V)h \end{aligned}$$

Model parameters leading to gain scaling



Model parameters leading to gain scaling



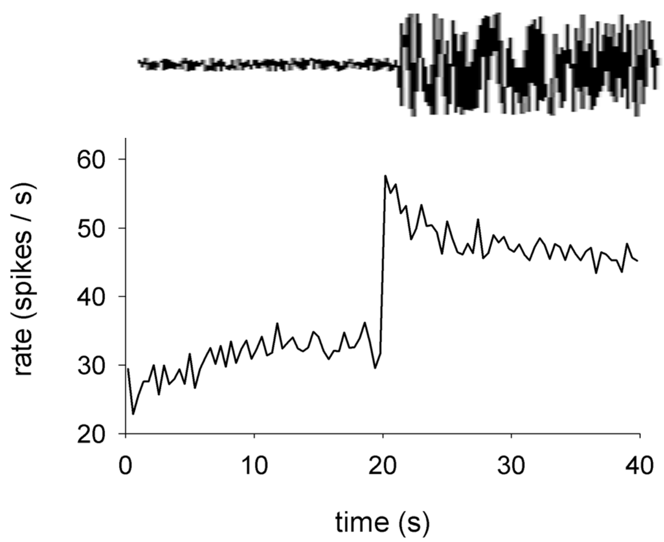
Gain scaling in single cortical neurons

- *Single neurons* exhibit stimulus normalization and thus can act as efficient encoders
- This property appears to emerge in cortical neurons over development
- Modeling shows that the nonlinearity of Na^+ and K^+ channels is sufficient to generate this behavior

Encoding natural signals

- Track stimulus statistics
- .. in order to best encode fluctuations
- *Encode the envelope*

Adapting firing rate encodes the envelope



Adaptation assumes estimation

Appropriate adaptation requires an estimation of the input statistics

There are costs to

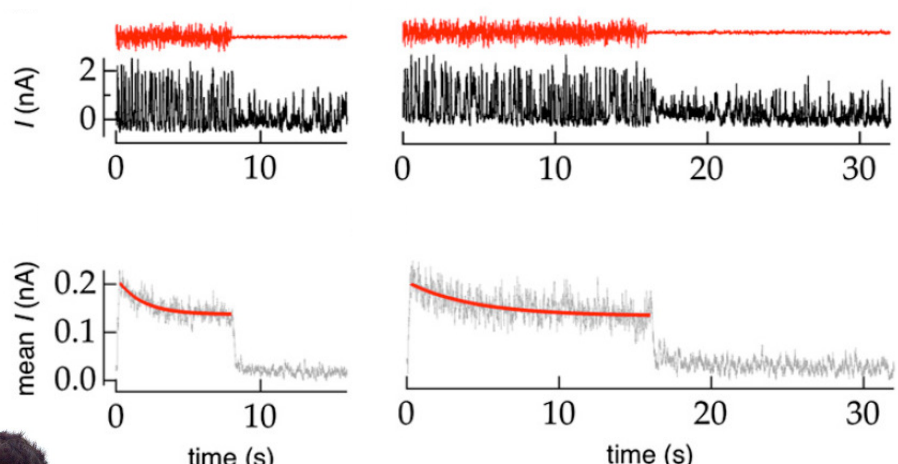
- ➢adapting too fast
- ➢adapting too slowly

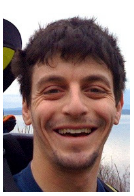
Speed/accuracy tradeoff

Is there an **optimal timescale for estimation** that determines timescales of adaptation?

How long does it take to adapt to a new stimulus condition?

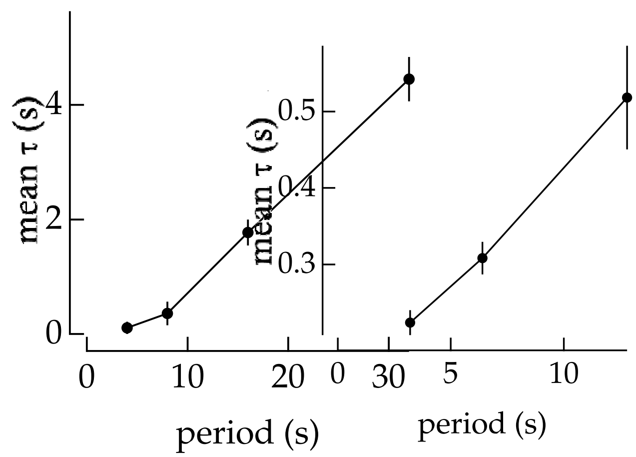
Timescales of contrast adaptation in mouse RGC inputs





Wark, Fairhall and Rieke, *Neuron* (2009)

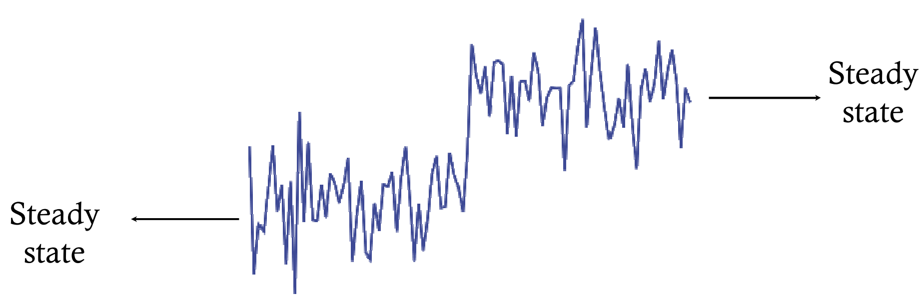
Multiple timescales of adaptation in RGC inputs



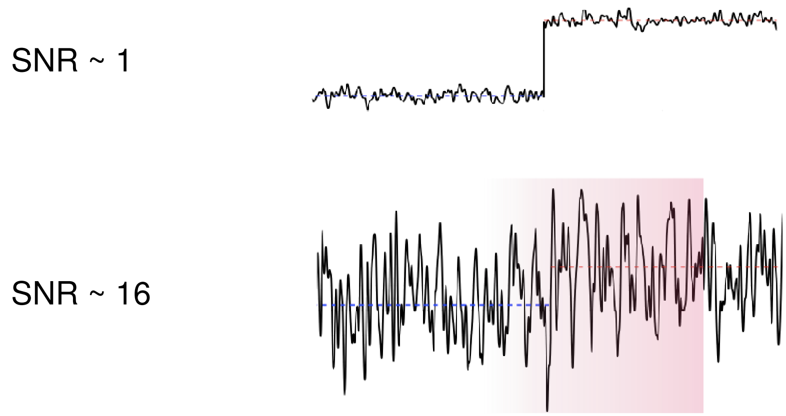
Variance (contrast) adaptation

Mean (luminance) adaptation

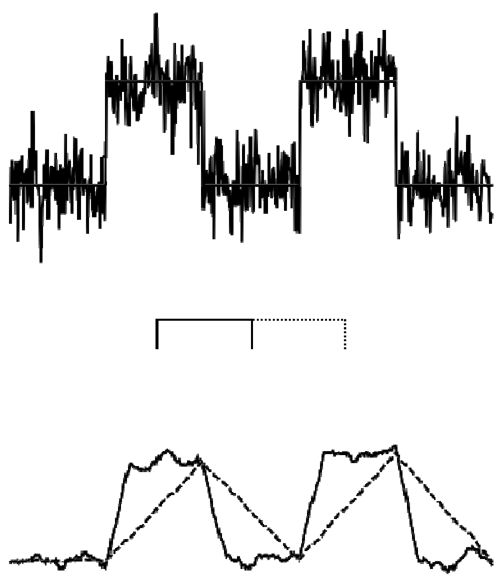
How long *should* it take to adapt to a new stimulus condition?



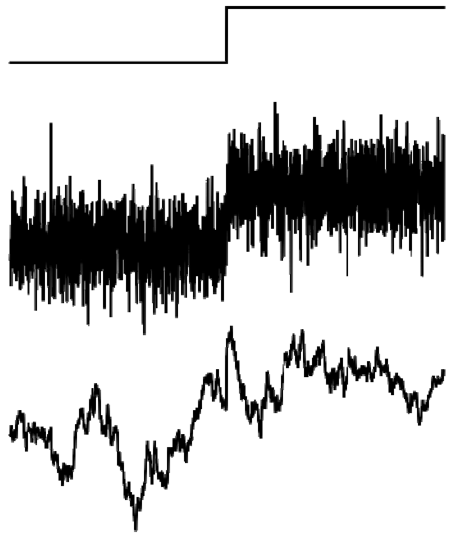
Noise level affects estimation time



Correlation time of luminance affects estimation time



Noise correlation time affects estimation time

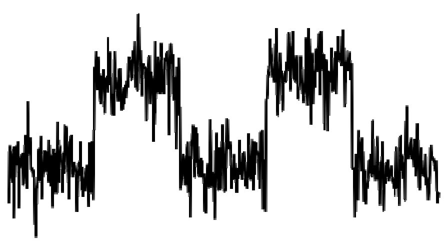


Short correlation τ_n

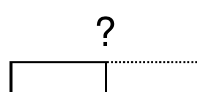
Long correlation τ_n

Finding the optimal luminance adaptation strategy

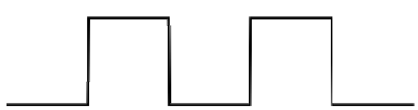
$s(t) = \mu(t) + \eta(t)$



$\gamma(t)$



$\hat{\mu}(t)$



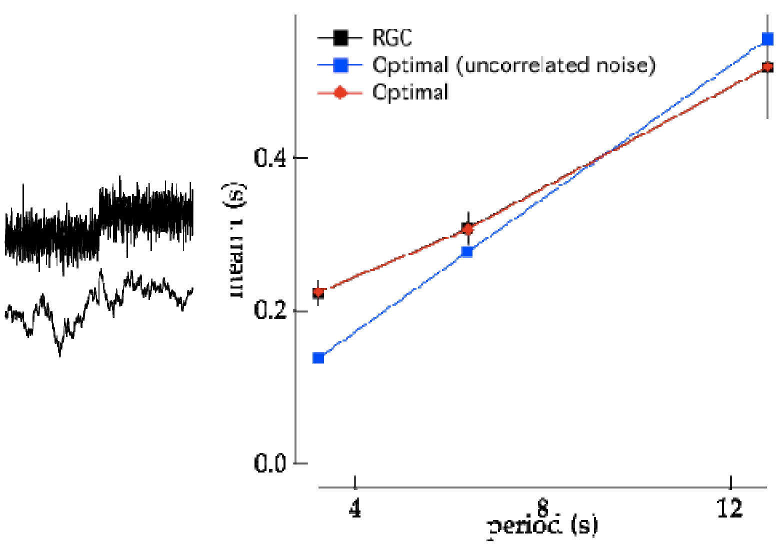
$$\hat{\mu}(t) = \int d\tau \; \gamma(\tau) s(t-\tau)$$

Predicted adaptation timescale

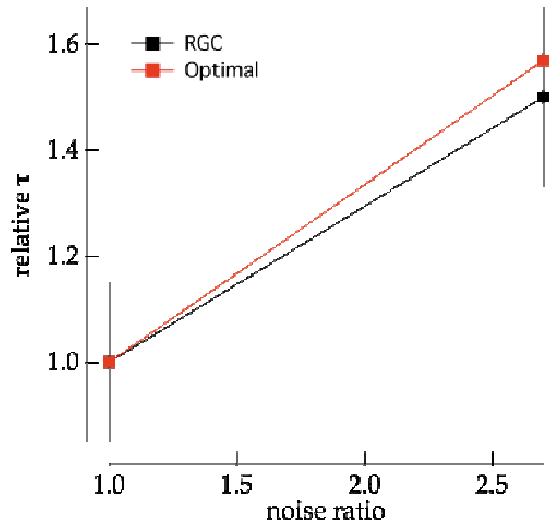
$$\tau_{\mathrm{adapt}} = \sqrt{\frac{\beta^2 \tau_\eta^2 + \tau_\mu^2}{\beta^2 + 1}}$$

$$\beta = \frac{\sigma_\mu}{\sigma_\eta}$$

Mouse retina is a nearly optimal adaptive encoder



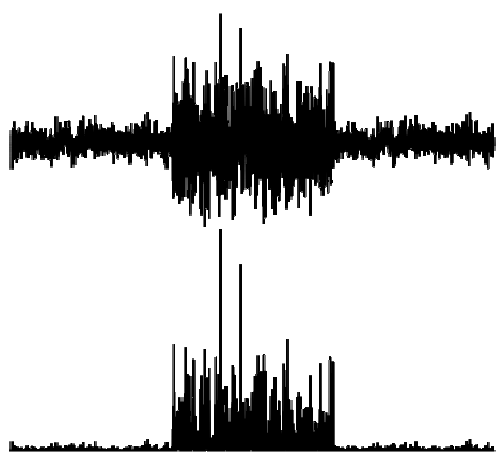
Filter predicts effect of noise on adaptation timescale



Finding the optimal variance adaptation strategy

$$s(t) = \boxed{\sigma(t)\eta(t)} + \xi(t)$$

$$s^2(t)$$

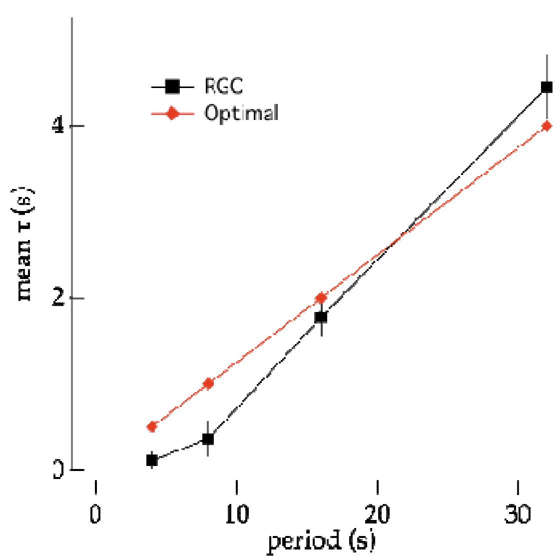


Predicted timescale of variance adaptation

$$\gamma(t) \propto e^{\frac{-2t}{\tau_\sigma}}$$

$$\tau_{\text{adapt}} = \frac{\tau_\sigma}{2}$$

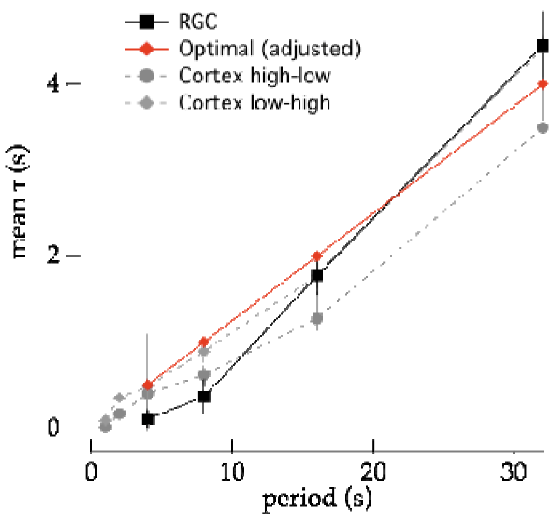
RGCs are nearly optimal estimators of stimulus variance



$$\gamma(t) \propto e^{\frac{-2t}{\tau_\sigma}}$$

$$\tau_{\text{adapt}} = \frac{\tau_\sigma}{2}$$

Depends only on stimulus, not system properties



Optimal timescales of adaptation

- The history dependence of adaptation can be accounted for by estimation models
- The rate of optimal variance adaptation may depend *only* on the correlation time of the variance envelope: the dynamics of variance adaptation may be conserved across systems and species.
- Under the conditions tested, mouse retina and rat cortex may be nearly optimal adaptive encoders
- Biophysical implementation: circuit, synaptic, membrane properties

Optimality through adaptive coding

- Different adaptive processes on different timescales help encode different temporal components of the signal

- Optimality provides a useful framework for interpreting and analyzing the phenomenology of adaptive neural coding

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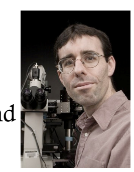

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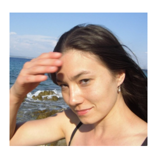

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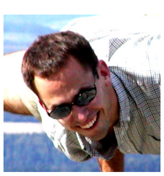

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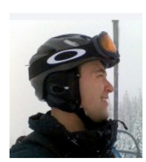

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